The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, NSW, Australia. Part 1: Bryophyta, Sphenophyta

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The bryophytes and sphenophytes in a rich and diverse megafossil flora from the Middle Triassic Nymboida Coal Measures of north-eastern New South Wales are described. The bryophyte material consists of two forms of liverwort-like thalloid plants. Sphenophytes are represented by both leafless and foliage bearing stems, dispersed nodal diaphragms and fructifications. Included are: *Zonulamites nymboidensis* gen. et sp. nov., a foliage bearing stem showing the attachment of basally conjoined leaves; *Nymbolaria tenuicaulis* gen. et sp. nov., which is the first record of a *Lobatannularia*-like plant from Gondwana and *Nymbotheca verticillata* gen. et sp. nov., an enigmatic fertile axis with possible affinities with the Discinitales, showing closely spaced verticillate discs bearing sporangial sacs over the whole disc surface. Doubt is expressed on a Gondwana presence of the genus *Neocalamites*

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Key Words: Palaeobotany, Middle Triassic, megafossil flora, Nymboida Coal Measures, Bryophyta, Sphenophyta.

INTRODUCTION

This paper provides the descriptive taxonomy of the bryophytes and sphenophytes in a rich and diverse megafossil flora preserved at two localities with similar facies and from approximately the same horizon in the Basin Creek Formation near the village of Nymboida in north-eastern New South Wales. The study will be completed in further parts comprising the ferns and fern-like foliage; pteridosperms and other gymnosperms. The fossil flora of these two assemblages will be referred to as the 'Nymboida Flora'. Previous references to fossil plants from Nymboida are in de Jersey (1958), Flint and Gould (1975), Retallack, (1977), Retallack et al. (1977), Herbst (1977), Webb (1980), Webb and Holmes (1982), Holmes (1987, 1992). For the present study all the material described in the papers above has been re-examined, with the exception of that of de Jersey (1958) which was apparently discarded after completion of the study.

The Nymboida Flora, while containing many previously undescribed taxa, has numerous elements in common with other *Dicroidium* assemblages that flourished throughout Gondwana during the Middle and Late Triassic. The Nymboida material is closely comparable with the megaflora from the Toogoolawah Group of the Esk Trough in south-eastern Queensland (Walkom 1924, 1928; Rigby 1977; Webb 1982, 1983) and with some assemblages of the well-studied Molteno Flora of South Africa (Anderson and Anderson 1983 and in prep.).

GEOLOGICAL SETTING

The Nymboida Coal Measures were described and mapped during a study of the Clarence-Moreton Basin by McElroy (1963). They are now included in the Nymboida Sub Basin which lies unconformably below the Triassic to Late Cretaceous non-marine sediments of the Clarence-Moreton Basin (O'Brien et al. 1994). The similarities of the fossil floral assemblages of Nymboida with those from the Toogoolawah Group of the Esk Trough of south-eastern Queensland suggest that the Nymboida Sub Basin was a contemporaneous southern extension of the Esk Trough (Fig. 1).

The Nymboida quarries described below, lie within the Basin Creek Formation which is the topmost unit of the Nymboida Coal Measures. The age of the Dalmally Basalt which lies below the Basin Creek Formation and above the Cloughers Creek Formation has been radiometrically dated at 237±0.4 million years (Retallack et al. 1993). Identical megafossil floras lie both above and below the Dalmally Basalt, thus indicating no significant time interval between the deposition of the two Formations (Retallack et al. 1977). Using the Time Scale of Menning (1995), the age of the Nymboida Flora is early Middle Triassic or Anisian.

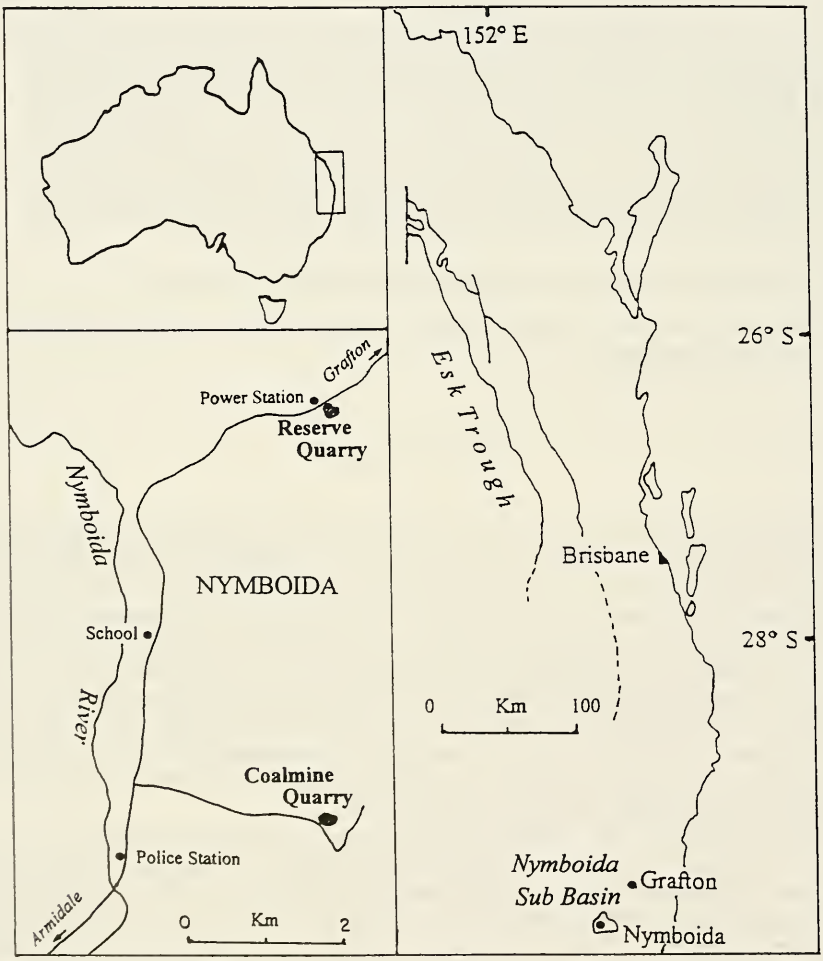

Figure 1. Map showing the Nymboida Sub Basin as the inferred southern-most extension of the Esk Trough; and the Nymboida District with location of fossil-bearing quarries.

Figure 2. (A). Coalmine Quarry, Nymboida. North-eastern face showing overlying massive sheet sandstone and a crevasse splay deeply incised into thinly bedded grey shales, siltstones, thin coal seams and fossil soil horizons. (B). Reserve Quarry, Nymboida. Northern face with a sheet sandstone overlying thin cyclic beds of sandstone, siltstone and coaly shales.

The plant fossil collections on which this study is based came from two brickpits or quarries near the village of Nymboida in north-eastern NSW (Fig. 1). Coalmine Quarry (Fig. 2A) is located near the crest of a ridge approximately 50 metres above and to the west of the site of the now abandoned Nymboida Colliery. The quarry, now also abandoned, had a working face of c. 20 metres and a floor area of c. 0.5 hectare. Retallack's reference to this quarry as the 'Nymboida Open Cut' (Retallack 1977) is confusing due to the Number One workings of the nearby Nymboida Colliery having been excavated as an open cut following a disastrous explosion in that section of the underground mine. Coalmine Quarry is listed as L1489 in the Locality Register of the Geology Department of the University of New England, Armidale and is the reference site for the Triassic vegetation associations of 'Dicroidietum odontopteroidium' and 'Phoenicopsetum' (Retallack 1977).

The photograph in Figure 2A shows the same vertical section of Coalmine Quarry as that illustrated by Retallack (1977), who noted the crevasse splay of coarse sandstone which was deeply incised in the underlying, well laminated shales, siltstones and palaeosols and the whole overlain by a massive sheet of sandstone.

The second site is an extensive shallow pit in the Three Mile Swamp Travelling Stock Reserve (Figure 2B). This locality will be referred to as the Reserve Quarry. The University of New England no longer maintains a Locality Register so this site is not recorded. Reserve Quarry is situated approximately 300 metres north-east of the road entrance to the Nymboida Hydro-Electric Station on the Grafton to Armidale Road. The quarry workings covered an area of approximately 2 hectares, but some of the area has been 'rehabilitated'. Due to the strata dipping at approximately 20° to the north, there have been several working faces each to a depth of three to five metres, with the result that a total of 15 to 20 metres of strata have been exposed.

While the two quarries are separated by the Shannon Fault and a lateral distance of c. 5.3 km, the similarity in lithology, facies, fossil assemblages and by a similar capping of a massive bed of sheet sandstone, suggests that their deposition may have been contemporaneous.

The sedimentary sequences displayed at both quarries represent overbank flooding events by a large meandering river onto an alluvial floodplain with open stagnant lakes and permanent swampland. Spring flooding from snowmelt on the high lands of the New England Fold Belt would have transported large quantities of sediments into the Nymboida Sub Basin which McElroy (1963) regarded as a ponded environment. The finely laminated grey shales in the quarries are an indication of seasonal flooding events. The irregular layers of coarse sandstone represent either abnormal high water flooding or migration of the main stream across the floodplain. A reconstruction of the Anisian Nymboida environment is illustrated in Retallack (1977).

Based on the Polar Wandering Path, reconstructions of Gondwana for the Early to Middle Triassic by Anderson and Anderson (1983), show the Nymboida region lying at c. 70° South. The proximity of the Palaeo-Pacific Ocean would have had an ameliorating effect on daily and seasonal temperature fluctuations thus creating a cool temperate climate and with moisture not a limiting factor. Banks of fossil leaves which occur on numerous horizons suggest that some, at least, of the vegetation was deciduous as an adaptation for coping with the low angle of sunlight and a long period of winter darkness.

Gulson et al. (1990) gave a qualified figure of 125 metres per 1,000,000 years for the rate of accumulation of sediments in the combined Permian Newcastle and Tomago Coal Measures. Assuming the same rate of deposition in the Nymboida Coal Measures, while acknowledging the diverse factors of climate and geography that may influence the rate, the sediments exposed in the Nymboida quarries could represent a time span of approximately 125,000 years. The Nymboida fossil collections provide a unique window onto the mosaic of plant communities and successions that occupied an area of 2.5 hectares during a brief period of geological time.

METHODS

Since 1966 I have made approximately 40 collecting trips to Nymboida, usually accompanied by my family who provided valuable assistance. By 1999 the Nymboida Collection numbered over 2,300 selected slabs with most displaying two or more fossil plants. This collection represents an invaluable sample and is the most comprehensive collection from any Australian Triassic locality. However, in spite of the large sample, even on the most recent trips, new taxa and material not previously observed have been discovered which indicates that there is still great potential for further discoveries, especially of fructifications from the many plants that are known only from dispersed leaves.

The two quarries that have yielded the Nymboida Flora were operated as brickpits and provided the raw material for the production of apricot coloured bricks by the Grafton Brickworks Company. Over a period of forty years, Mr Brian Foley, an earthmoving and trucking operator, single-handedly excavated and transported all the material, estimated in excess of a million tonnes, from Nymboida to the brickworks at Grafton. Mr Foley's co-operation during visits to the quarries greatly assisted in the collection of many important specimens.

Explosives were sometimes used to fracture sections of the quarry faces which collapsed to form an easily excavated mass of rubble. Most of the collections were made from fallen blocks on the quarry floor and it was not possible to establish the exact horizon from which the material originated. Therefore it is difficult to recognise palaeodeme assemblages such as those recorded by Anderson and Anderson (1983) in their Molteno vegetation studies.

The high content of the expanding clays, montmorillonite and illite, in the naturally wet shales in both quarries created problems in preserving the fossils. Split fossiliferous shale slabs, when exposed to the sun and wind, dried rapidly and cracked into small fragments. The problem was solved by wrapping the fossil slabs immediately on exposure in several layers of newspaper and leaving to dry naturally over a period of several weeks. After unwrapping, even the largest slabs would remain indefinitely in a stable condition as long as they were kept dry. Each slab received a painted serial number and was sorted into broad categories such as sphenophytes, ferns, *Dicroidium,* cycads etc. and stored in racks in redwood boxes formerly used by the Australian Museum for its early fossil collections.

For comparison and study, relevant material is sorted, laid out on benches and examined with a Nikon 10X-50X binocular microscope. Significant specimens are photographed using low angle sunlight or with artificial lighting. Some are photographed under kerosene to enhance contrast. Where possible the range of variation within a taxon will be illustrated. Figures of specimens are natural size unless otherwise indicated.

Type material plus all illustrated and mentioned specimens receive AMF numbers and are housed in the Palaeontological Collections of the Australian Museum, Sydney.

The Nymboida fossil material consists of apparently well preserved carbonaceous compressions in siltstones and shales and as impressions in coarser sediments. De Jersey (1958) and Hennelly (in McElroy 1963) were able to obtain only scarsely recognisable pollen grains and spores in a highly oxidised form from the Nymboida Coal Measures although McElroy (1963) reported the presence of well-preserved cellular structures in thin sections of vitrinite from the Cloughers Creek Seam within the Basin Creek Formation. Despite numerous attempts, I have been unable to obtain cuticle with preserved cell structure from the carbonaceous compressions. On maceration, the most promising-looking material disintegrates into structureless fragments. Cellulose pulls and transfers reveal only the crystalline or cleat structure of the organic material which has been converted into high rank coal as a result of a tectonic heating event during the Cretaceous Period (Russell 1994).

SYSTEMATIC PALAEOBOTANY

Phylum Bryophyta
Class Hepaticopsida

Liverworts occur sparingly throughout the fossil record, the earliest being from the Upper Devonian of New York (Hueber 1961). Liverworts and indeterminate thalloid remains have been recorded from the Triassic of Gondwana by Townrow (1959, 1964), Jain and Delevoryas (1967), Anderson (1976) and Webb and Holmes (1982). The paucity of these fossils is partly explained by Lacey (1969) who suggested that the chance of preservation depended not so much on the conditions suitable for growth of bryophytes or the possession

of resistant structure, but on the occurrence of the right kind of sedimentation at the right place and time. Scattered fragmentary remains and occasional colonies of *in situ* thalloid plants occur in the Nymboida quarries.

While the essential diagnostic characters of air chambers, ventral scales or rhizoids can not be observed in the Nymboida material, the growth pattern and gross morphology of the thalli is highly indicative of the fossils being liverworts.

The confusion arising from the continued use of the generic name *Thallites* to include thalloid plants with insufficient preservation to allow for closer identification was discussed by Webb and Holmes (1982). They concluded that there was no justification for continuing to use a name which caused nomenclatural problems and was of no practical use. Later, Oostendorp (1987) provided a historical review of fossil liverworts and discussed the form genera used for specimens whose preservation does not allow for an accurate classification. Under Oostendorp's classification, the Nymboida material described below would be placed in either *Thallites* or *Hepaticites*. However the nomenclatural problems raised by Webb and Holmes (1982) are still relevant. Therefore I place the Nymboida liverwort-like specimens under the non-committal term of 'Thalloid Fossil'.

Thalloid Fossil sp.A
Figs 3A-E, 4A.

Description

Thalloid rosettes to 6 cm in diameter, consisting of three or more limbs radiating from a central point; branching dichotomously at angles varying from 45° to 75°. Proximal portion of limbs 2 - 3 mm wide, margins smooth. Thick carbonaceous material along the centre line of the limbs gives a midrib-like appearance. The outer portion of the lamina is of more delicate texture and often appears to be translucent. Distal end of limbs possibly emarginate but mostly broken or missing.

Material

AMF112467-72 from Reserve Quarry, Nymboida, Basin Creek Formation.

Discussion

Rare fragments of this type of thallus occur at the Coalmine Quarry. In the Reserve Quarry some bedding plane surfaces of the finer grained sediments are covered with closely spaced rosettes of this plant to the exclusion of all other plant material. Obviously these were liverwort-like pioneering plants colonising a bare mud surface of flood sediment deposited under still water conditions. The plants were preserved *in situ* when further mud was deposited during a subsequent flooding event. The preservation of these thalli is such that diagnostic features required for their specific identification as liverworts is missing. However from their gross morphology I believe these are liverworts and perhaps, allied to the Marchiantales (cf. Anderson 1976).

Thalloid Fossil sp.A differs from the few liverworts recorded from the Gondwana Triassic. *Eomarchantites cyathodoides* (Townrow) Schuster (Townrow 1959, Anderson 1976, Krassilov and Schuster 1984) differs by its smaller size. *Marchantites tennantii* Anderson (1976) has a smaller thallus, undulate margins and possible fertile structures at some lobe apices. *Thallites* sp. (Jain and Delevoryas 1967) from the Cacheuta Formation of Argentina is too fragmentary for comparison.

Thalloid Fossil sp.B
Figs 4B,C.
Indeterminate thalloid fossil sp.B, Webb and Holmes 1982, p86,Fig.2a; pl.7, fig.4.

Description

A thalloid rosette with about 8 branches radiating from a central point, each branch dividing several times, proximally into 3 or more divisions and pseudodichotomously at the distal portions of the thallus to form numerous terminal lobes. Apices not known. Branches and lobes c. 1 mm wide but broader at the proximal divisions. Carbonaceous material preserved evenly across the branches and lobes; no apparent midrib.

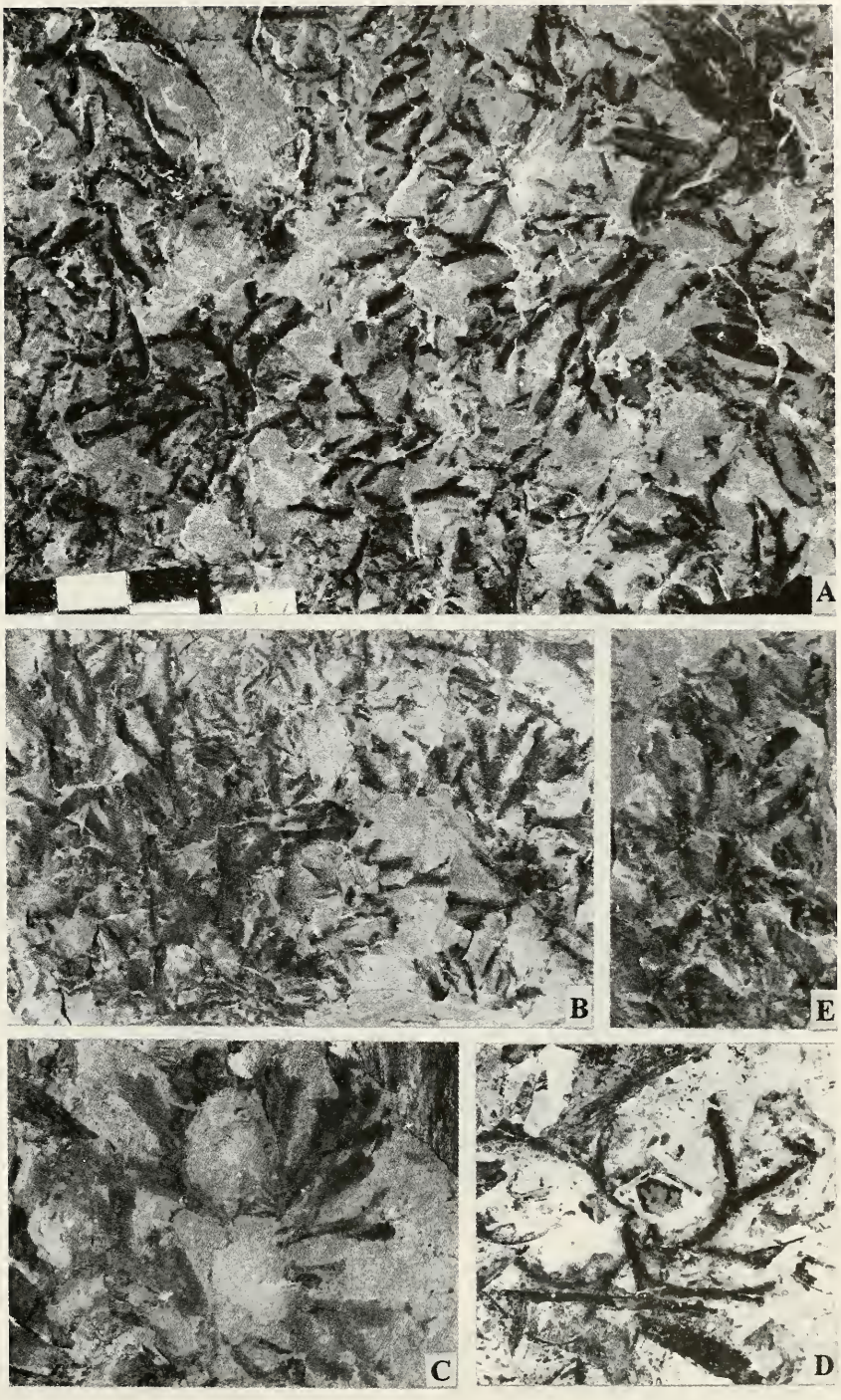

Figure 3. Thalloid fossil sp.A. (A). AMF112467. (B). AMF112468. (C). AMF112469. (D). AMF113371. (E). AMF113372. All from Reserve Quarry.

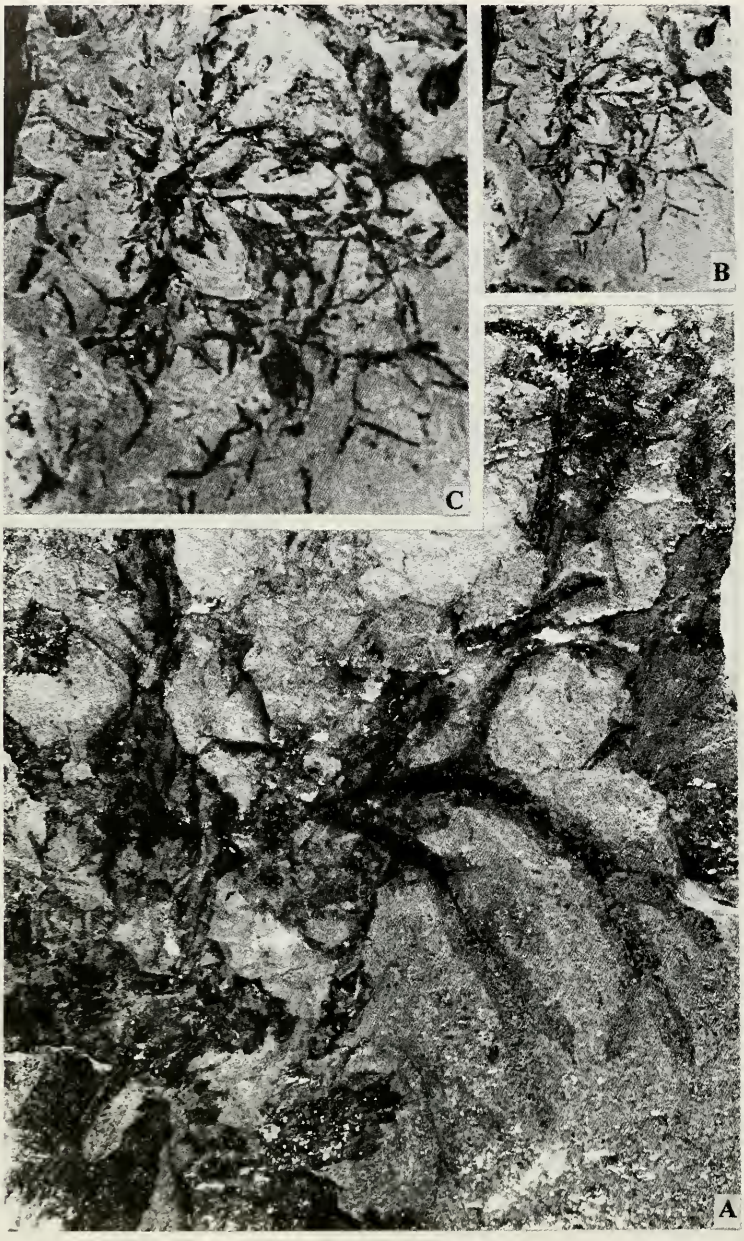

Figure 4. (A). Thalloid fossil sp.A.AMF113370, x2, Reserve Quarry. (B). Thalloid fossil sp.B. AMF61703, (C). AMF61703 x2. Coalmine Quarry.

Material

AMF 61703 - from Coalmine Quarry, Nymboida, Basin Creek Formation.

Discussion

This is a rare thalloid fossil with only a single rosette and some fragmentary remains in the collections. The method of branching distinguishes this specimen from all other Gondwana thalloid plants.

Phylum Sphenophyta
Class Sphenopsida

Fossil remains of equisetalean stems occur worldwide in Triassic freshwater lacustrine margin and swamp facies (Boureau 1964). On some horizons they may form the dominant vegetation (Harris 1926, Anderson and Anderson 1983).

The Nymboida collections include dispersed nodal diaphragms, equisetalean stems, both with and without attached foliage and associated fertile structures. Some horizons at the Reserve Quarry are covered with mats of poorly preserved stems and foliage. At Coalmine Quarry sphenophytes remains are rare and dispersed. However, some of that material is well preserved and adds to our knowledge of the diversity of Gondwana sphenophytes. The new material is here placed in form genera with the hope that future collecting will provide evidence to reconstruct whole plants.

Order Equisetales
Genus *Zonulamites* nov. sedis incertae
Type species *Zonulamites nymboidensis* gen. et sp. nov.

Generic diagnosis

A foliage-bearing *Paracalamites*-type stem with linear leaves conjoining near base to form a short continuous sheath at the node; more internodal vascular bundles than number of leaves in a whorl.

In this diagnosis the features of the conjoining of the leaves to form a sheath and the lack of transverse striations distinguishes *Zonulamites* from *Neocalamites* (Halle 1908).

Zonulamites nymboidensis gen. et sp. nov.
Figs 5A-E, 6A-B.

Diagnosis

A *Zonulamites* with long linear, often rigid, leaves with four or more longitudinal striations or wrinkles; no midrib. Stem expanded at the nodes which are marked by a transverse groove just above the base of the leaf sheath. Exterior of stem smooth or irregularly striated. Vascular bundles forming closely spaced ribs on the interior surface of the hollow stem internodes; with a ratio of leaves to vascular bundles of one to three.

Description

The holotype (Fig. 5A,B) is an impression showing the external features of a portion of a stem 140 mm long with three nodes at which leaves are attached. The stem is c. 12 mm wide with nodal regions slightly expanded; internodes variable in length, from 40 - 70 mm. The external internode surface is irregularly striated but without well-defined longitudinal ribs and grooves. Leaves of apparent thick texture; about 20 in a complete whorl; length in excess of 60 mm but all are incomplete; apices unknown; width 1 - 2 mm, mostly c. 1.5 mm. Leaves attached parallel to the stem or at a very high angle then remaining rigid and almost perpendicular or decurving; without a midrib but marked with four or five longitudinal striations or wrinkles which may be the result of shrinkage before or during preservation. Near the base, each leaf expands laterally to conjoin with the adjacent leaves to form a continuous sheath 3 - 5 mm long. The position of the node is marked by a distinct horizontal groove, below which the leaf sheath continues for another 1 - 2 mm.

Figure 5C is a partially decorticated stem with leaf bases clearly conjoined into a sheath. Figure 5D is a stem 12 mm wide that has been compressed vertically, resulting in considerable shortening of the internodes. The swelling at the nodes in this specimen and the holotype suggests the internal presence of well-developed nodal diaphragms. Fig. 6A is a large compressed stem 30 mm wide, with three nodes and an internodal length of c. 60 mm. The upper portion is an external mould showing a smooth surface; the lower portion is an internal cast showing fine longitudinal ribs and grooves. The lower node shows

circular scars c. 0.75 mm in diameter and a ratio of the number of scars to ribs of one to three. At the top of the same stem the enclosing sediment has broken to reveal a whorl of incomplete leaves attached to the stem (Fig. 6B). The leaves, c. 1.5 mm wide, expand and conjoin towards the base. The base of the leaves appears to be triangular or deeply grooved in cross section.

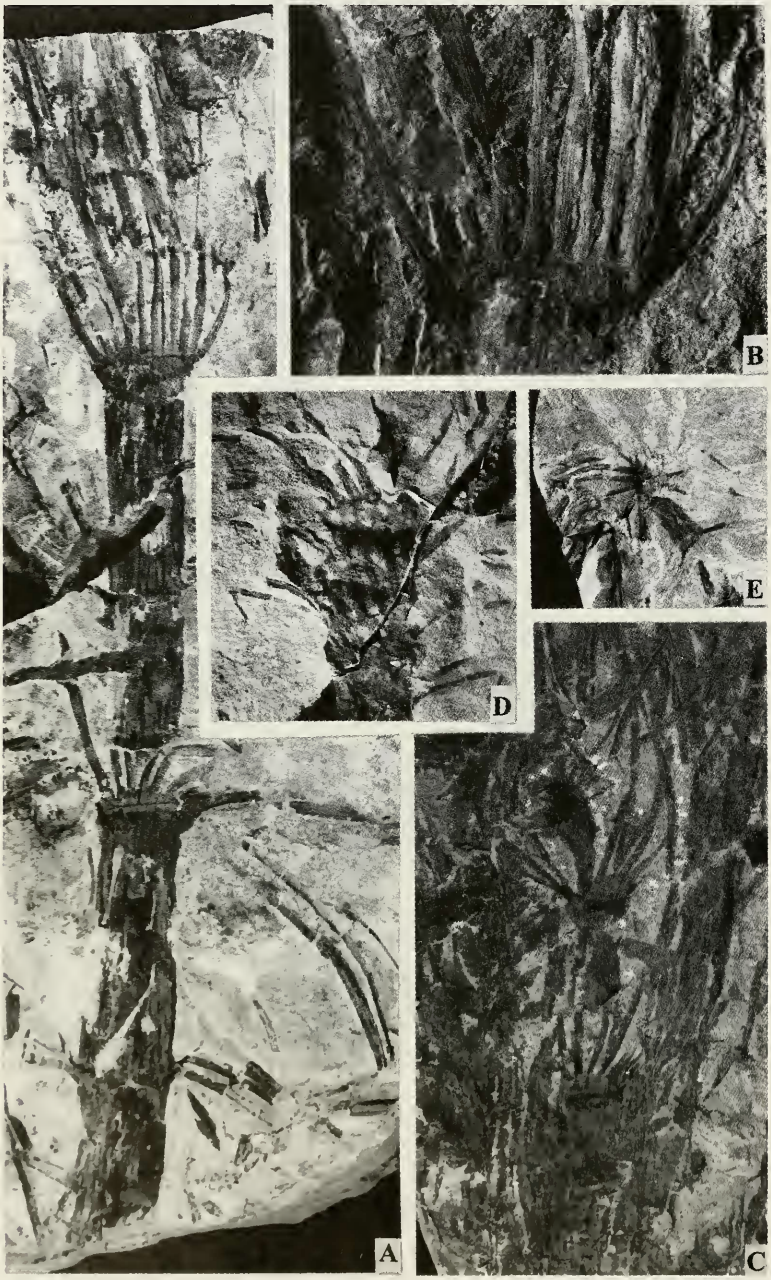

Figure 5. *Zonulamites nymboidensis* gen. et sp. nov. (A). Holotype, AMF112474. (B). AMF112474 x2. (C). Partially decorticated stems with intact foliar sheaths. UNEF13399. (D). Vertically compressed stem. AMF112476. (E). Detached leaf whorl. AMF112475. All from Coalmine Quarry.

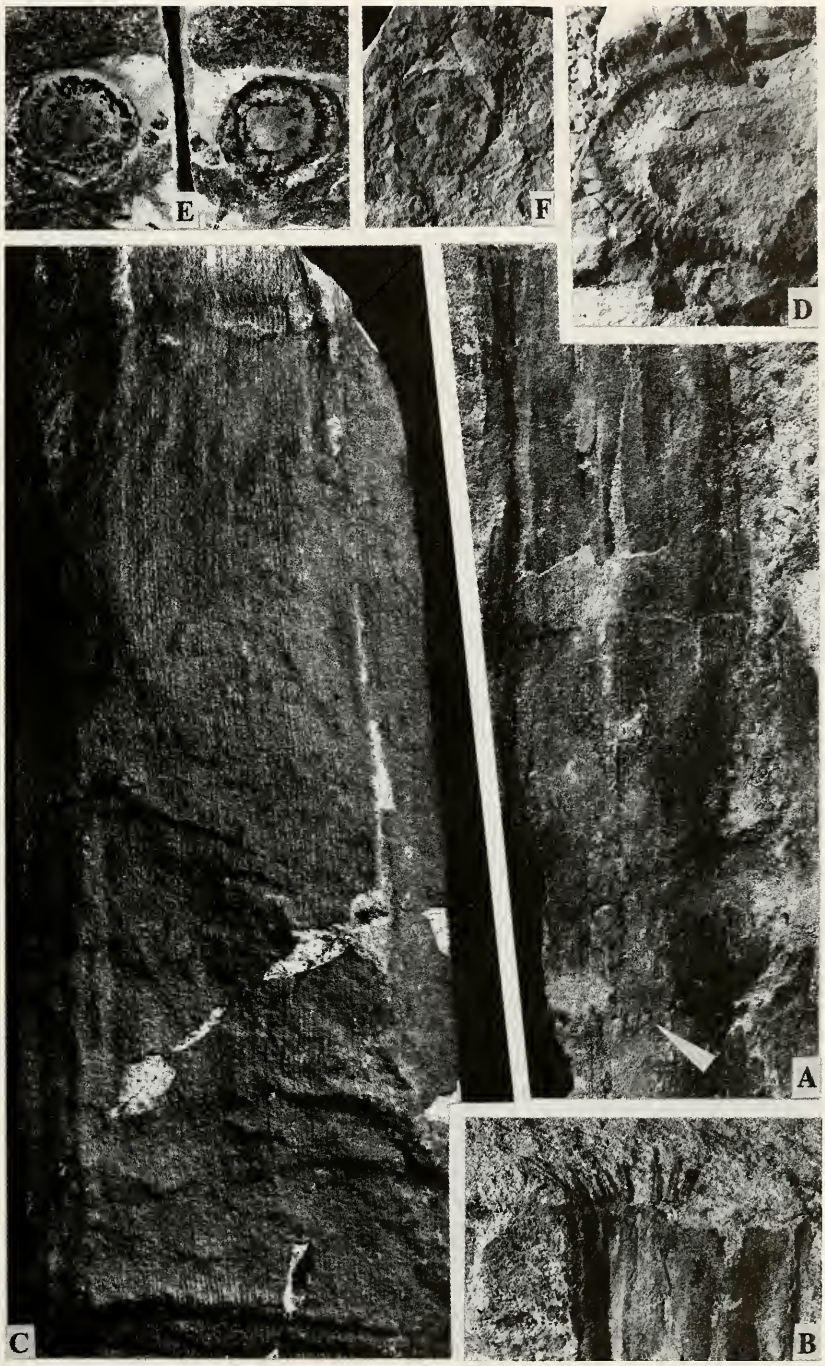

Figure 6. (A&B). *Zonulamites nymboidensis* gen. et sp. nov. AMF112474. A). A large stem showing in lower portion an internal cast of vascular bundles and leaf scars (arrowed), the upper portion is an external cast of the outer surface of the stem. B). Same specimen with portion of an attached leaf whorl. (C&D). *Paracalamites* sp.A. C). AMF112479. Three dimensional internal cast of large stem with two nodes. D). AMF112485. Transverse section of a stem. (E). *Nododendron* sp.A. AMF112483. Part and counterpart of a nodal diaphragm. (F). Nodal diaphragm sp.B AMF112477. All from Coalmine Quarry.

Holotype

AMF112474 Australian Musem, Sydney. Paratypes, AMF112475-6, AMF112484, University of New England F13399.

Type Locality

Coalmine Quarry, Nymboida, Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Name Derivation

zonula - Latin, little girdle; - *mites* - an abbreviation of *Calamites*, to suggest affinities with other equisetalean leaf-bearing stems.

nymboidensis - from Nymboida.

Discussion

The illustrated specimens demonstrate the conjoining of the linear leaves in a whorl to form a short sheath encircling the stem at the node, a feature that can be seen only in well-preserved compressions or external impressions. The number and width of leaves in each whorl is variable and related to the stem diameter. The irregularly striated leaves which show no midrib appear to be flat or slightly keeled in cross section and there is no evidence as to the organisation of the foliar vascular system. There are no articulations along the length of the leaves that would suggest that these organs may have been branches as in *Nododendron suberosum* Artabe and Zamuna (1991) (but see Holmes in press), or cladophylls as in undescribed material from the Molteno Formation of South Africa (H.M. Anderson pers. comm.).

The genus *Neocalamites* Halle (1908) was erected for Northern Hemisphere equisetalean plants in which the longitudinal ribs on the internodes did not alternate at the nodes as in *Calamites* and *Equisetum* and the verticels of linear leaves were free to the base. Many species of *Neocalamites* have been described (Boureau 1964). They have been based often on morphological features that may be extremely variable and overlapping, for example, in the density of ribs on the internal casts, ratio of diameter to internode length and the width and number of leaves in a whorl (Kawasaki 1939). Many Gondwana Triassic equisetalean plants that exhibited only superficial similarity in gross morphology have been placed in *Neocalamites* species originally described from Northern Hemisphere material. In Gondwana assemblages, fossil equisetalean stems are often numerous but foliage bearing axes that clearly demonstrate the leaf attachment are very rare. I have examined the Australian material assigned to *N. carrei* (Walkom 1915; Hill et al. 1965) and *N. hoerensis* (Walkom 1915, 1924; Jones and de Jersey 1947; Retallack 1977; Playford et al. 1982; White 1986). In none of these specimens are details preserved of the leaf bases or the attachment of the leaves to the stem.

In contrast to Northern Hemisphere *Neocalamites* plants which lack or have poorly developed nodal diaphragms (Harris 1961; Kimura et al. 1982), well-developed and persistent nodal diaphragms are present in many Gondwana Triassic assemblages (Walkom 1925; Frenguelli 1949; Hill et al. 1965; Retallack 1973; Anderson and Anderson 1985 and Holmes in press). The nodal diaphragms figured by DuToit (1927); Frenguelli (1949); Artabe and Zamuner (1991) and Holmes (in press) are encircled by persistent leaf bases which appear to coalesce and shortly conjoin to form a narrow sheath as in *Zonulamites*.

Harris (1961) indicated that several features of Gondwana sphenophytes that had been placed in *Neocalamites hoerensis* differed from the Northern Hemisphere *N.hoerensis* sensu Halle (1908). Based on this, Retallack (1980) suggested that the Gondwana plants should be placed in a new species of *Neocalamites*. I believe that the considerable extension of the diagnosis required for *Neocalamites* to embrace the factors of the robust diaphragms and basally conjoined leaves that are present in the Gondwana material would cloud the evidence pointing to phytogeographical separation of two groups of not closely related plants that occupied similar ecological niches in the Northern Hemisphere and Gondwana during the Triassic Period. The *Neocalamites* genus may not be as cosmopolitan in its distribution as previously thought (Boureau 1964).

Fragmentary equisetalean leafy stems and isolated leaf whorls from the Brookvale

Shale Lens in the Hawkesbury Sandstone of the Sydney Basin were described as *Phyllotheca brookvalensis* by Townrow (1955) although he considered they did not fit comfortably in any existing genus. On the basis of the leaves conjoining at the node and the possible presence of a minute sheath, he placed the material doubtfully in *Phyllotheca* rather than *Neocalamites* from which it differed by the presence of a complex node and by having only one vascular bundle per leaf. Holmes (in press) has transferred *Phyllotheca brookvalensis* to a new genus *Townroviamites*. The transversely compressed leaf whorl illustrated here (Fig. 6E) is superficially similar to some of Townrow's material. However *Zonulamites* differs from *Townroviamites brookvalensis* by the absence of a leaf midrib and by the presence of three internodal vascular bundles to each leaf.

I have examined the Argentinean Triassic sphenophyte collections held in the Museo Argentino de Naturales Ciencias 'Bernardo Rivadavia', Buenos Aires and the Museo de La Plata, La Plata. At the former institution a group of specimens (11752-4) from the El Tranquilo Formation of Argentina are similar to *Zonulamites*. The poor state of preservation of the Types held in the Museo de La Plata of *Neocalamites ramaccionii* (Frenguelli 1944a, specimens 10870-2) and *Neocalamites ischigualasti* (Frenguelli 1944b, specimens 10880-1) does not allow for comment on the validity of the generic placement of these specimens. A nodal diaphragm (La Plata 11125) placed in *Equisetites fertilis* by Artabe (1985) bears a close resemblance to the *Nododendron* diaphragms from Benolong, NSW (Holmes in press) which are associated with stems similar to *Zonulamites*.

I suggest that all Gondwana sphenophyte foliage-bearing stems that have been placed previously in *Neocalamites* or *Phyllotheca* be re-assessed for possible inclusion in *Zonulamites* or *Townroviamites.*

Equisetalean Leaf-bearing Stems cf. *Zonulamites* sp.
Fig. 7A

Discussion

Some horizons in the Reserve Quarry are packed with the compressed remains of a monoculture horsetail thicket. None of the material is preserved in its upright position of growth (cf. Kimura et al. 1982) but the quantity of stems with leaves still attached indicates that these are at least, semi-autochthonous deposits. The fossil assemblages on the bedding planes give the impression of a mass of vegetation that has been overwhelmed and preserved under flood deposited silt. The stems vary in width from less than 10 mm to more than 20 mm. Incomplete stems over 1 metre in length have been observed on exposed blocks. The external surface of the stems is smooth or irregularly ribbed, some showing four or five longitudinal ridges and hollows which are too broad to represent the number of vascular bundles in the interior walls of the stems. This is perhaps an artifact caused by the collapse of the hollow stems during preservation and is not related to the physiology of the living plants. The expanded nodal regions in some stems suggests the presence of well-developed nodal diaphragms. Internodal lengths vary according to the position up the stem. Near the apex the closer whorls of leaves form an overlapping mass of foliage. The linear leaves, without a midvein, range from 1 mm to 1.5 mm wide and to over 60 mm long. All leaves are incomplete and no apices are known. Leaf bases and method of attachment of the leaf whorl to the node is not preserved. In the holotype of *Zonulamites nymboidensis* the stem and leaf widths are similar to those in these mass assemblages, but while the type differs by its longer internodal length the range of variability within a population is not known. It is probable that these mass assemblages belong in *Zonulamites.*

Material

AMF11248, Reserve Quarry.

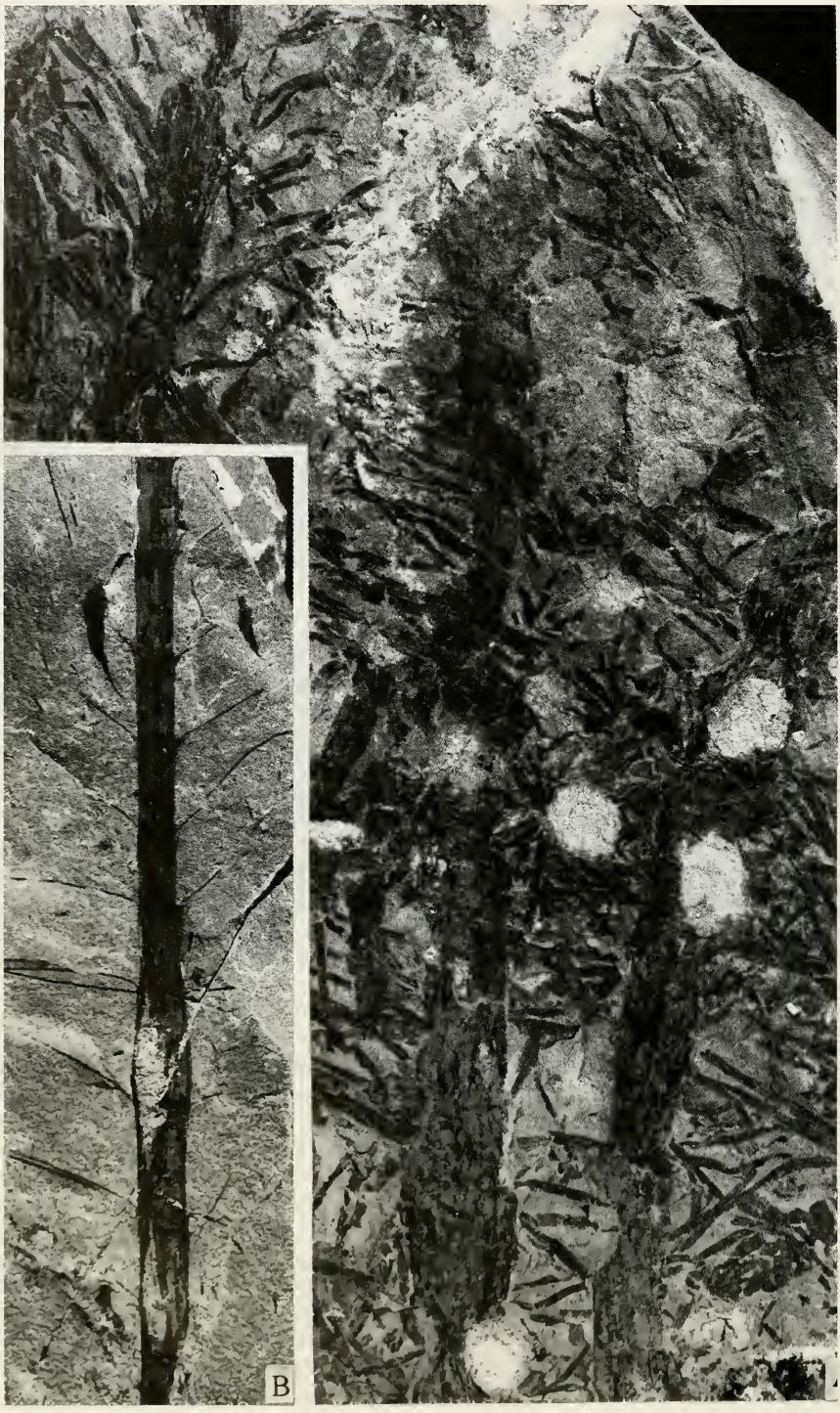

Figure 7. (A). ?*Zonulamites* sp.A. AMF112488. Portion of a large slab of equisetalean leaf-bearing stems. (B). *Townroviamites* ?*brookvalensis*. AMF112486. Both from Reserve Quarry.

Genus ?*Townroviamites* sp.A.
Fig. 7B.

Description

Two slabs with counterparts show portions of what may be the stem of the same plant. The stem is preserved as an internal cast is over 230 mm long, with base and apex missing. The width of the stem decreases from 7 mm to 5 mm over the length preserved. Nine well defined ribs and grooves traverse the full length of the stem without alternation at the nodes. The stem is slightly enlarged at the nodes which appear as horizontal ridges. Internode length decreases distally from 20 mm to c. 13 mm. A linear leaf is shown attached at an angle of from 45° to 60° at either side of each node. The incomplete leaves, with apices missing, may be in excess of 25 mm long. The width of the apparently very narrow leaves is c. 0.5 mm, but this may be a measure of the thickness of the leaf if it is exposed in longitudinal section. Each leaf expands slightly at the base and is decurrent on the stem. The fossil has not been excavated to determine whether there is a three-dimensional preservation of a leaf whorl within the matrix. The number of vascular bundles in the stem as estimated from the number of ribs and grooves in the cast is c.18. Related to the possible narrowness of the leaves, it appears that this plant may have the same number of leaves at the node as vascular bundles.

Material

AMF112486-7, Reserve Quarry.

Discussion

This is the only representative of this form of equisetalean so far collected at Nymboida. There appears to be the same number of leaves as vascular bundles. This feature is diagnostic for *Townroviamites*, but as the leaf bases and their form of attachment to the node is not known, this specimen is referred only doubtfully to that genus. The differences between *Townroviamites* and *Zonulamites* were discussed previously under *Zonulamites*.

Form genus *Paracalamites* Zalessky 1932
Paracalamites sp. indet.
Fig.6C, 6D

Description

Figure 6C is a fragment of a large stem preserved as a three dimensional sandstone-filled internal cast, c. 180 mm long, with two nodes, the lower forming a conspicuous groove c. 3 mm in width. The internode, 150 mm long and 60-70 mm wide, is marked by fine longitudinal ribs and grooves which do not alternate at the node. Density of ribs, c. 15 per 10 mm.

Discussion

This internal cast of a stem shows a similar density of vascular bundles to that in the large stem of *Zonulamites* in Figs 6A,B, but without other identifying features it is best placed in the form genus *Paracalamites.*

Zalessky (1932) instituted the form genus *Paracalamites* for equisetalean stem casts without foliage or fertile organs, but with internodal ribs continuing across the node without alternation. I follow Rigby (1966) in referring the Nymboida stem casts to this non-committal genus. To place them in *Paracalamites foxii* as proposed by Lele (1956) or *P. australis* McLoughlan (1992) would imply a conspecificity that may not exist.

Stems similar to the above have been recorded by Seward (1903), Walkom (1915, 1924, 1925), Chapman and Cookson (1926), Lele (1956) and Jain and Delevoryas (1967). Figure 6D is a transverse section of a stem with an internal ring of vascular bundles that are represented by the internal ribs at a spacing of c. 8 per 10 mm which is coarser than those shown in Fig. 6C.

Material

AMF112479 and AMF112485 both from Coalmine Quarry.

Equisetalean Nodal Diaphragms

Nodal diaphragms are very rare in the Nymboida Flora. So far, only two specimens of nodal diaphragms, each of a different form, have been collected from the Coalmine Quarry and none from Reserve Quarry despite the occurrence there of some horizons packed with *Zonulamites*-like plants.

Genus *Nododendron* sp.A
Fig. 6E

Description

Shown in the one photograph are the part and counterpart of a nodal diaphragm c. 18 mm in diameter. The central pith disc, 8 mm in diameter, is surrounded by a ring 1 mm in width of c. 40 carbon-filled depressions that represent vascular bundles. A smooth cortical collar surrounds the vascular bundle ring. No collar of leaf bases or sheath is preserved around the node.

Material

AMF112483

Discussion

This small nodal diaphragm bears some resemblance to *Nododendron suberosum* Artabe and Zamuner (1991) and *Nododendron benolongensis* Holmes (in press) but the preservation does not allow for specific comparison. The diaphragm of *Neocalamites ischigualasti* as described by Frenguelli (1944b) had a ring of vascular bundles around the pith disc and surrounded by cortical tissue much broader than this Nymboida node, but his type specimen no longer shows details of any nodal material.

Artabe and Zamuner (1991) reviewed the material described by Frenguelli (1949) as *Neocalamites hoerensis* and erected *Nododendron suberosum,* a new genus and species, to include both the external features of a stem and the ?internal features of the associated but separate nodal diaphragm. This raises nomenclatural problems for classifying isolated stems or nodes with only external features of gross morphology preserved. As discussed by Holmes (in press) the use of the form genus *Nododendron* should be restricted to nodes only.

Nodal Diaphragm sp.A
Fig. 6F

Description

A nodal diaphragm 16 mm in diameter, with a smooth pith disc 6 mm in diameter. Surrounding the disc is a cortical ring of about 20 wedge shaped segments. No carinal or vallecular canals or vascular bundles present.

Material

AMF112477

Discussion

This nodal diaphragm differs from *Nododendron* sp.A by the wedge shaped segments surrounding the pith disc and by lacking vascular bundles. It is closely similar to the nodal diaphragm of Holmes and Ash (1979, Fig. 3.5) from the Early Triassic Lorne Basin and to the nodal diaphragm from the Narrabeen Stage of the Sydney Basin which was included by Walkom (1925) with stems he placed in *Phyllotheca australis*. *Phyllotheca* is essentially a Permian Gondwanan plant genus and persistent nodal diaphragms appear to be absent from the Permian material. The nodal diaphragm referred to *Neocalamites* cf. *carrerei* by Hill et al. (1965) differs by the more numerous radial plications or wedges surrounding the pith. Robust nodal diaphragms are present in extant *Equisetum* (Foster and Gifford 1974) and are associated with Mesozoic material placed in *Equisetum* or *Equisetites*. Gondwana Triassic nodal diaphragms referred to *Equisetites* (Walkom 1915; Frenguelli 1944d; Jain and Delevoryas 1967) differ from the Nymboida specimens by the ring of circular protuberances around the perimeter of the relatively broad pith disc.

The silicified nodal diaphragms from the Transantarctic Mountains of Antarctica, *Spaciinodum collinsonii* (Osborn and Taylor 1989) differ from both *Nododendron* sp.A and Nodal Diaphragm sp.A by their smaller external diameter; by the relative larger diameter of the transverse sections of the vascular bundles and by the presence of cortical vallecular canals.

Figure 8. *Nymbolaria tenuicaulis* gen. et sp. nov. (A). Holotype. AMF112489. (B). Paratype AMF112490. (C). Paratype. AMF112491. A,B from Coalmine Quarry; C from Reserve Quarry.

Genus *Nymbolaria* nov. sedis incertae
Nymbolaria tenuicaulis gen. et sp. nov.
Figs 8A-C

Combined Diagnosis

Sphenopsid with slender ribbed stems bearing at each node pseudo-verticels of narrow lanceolate or elliptical leaves separated to the base and aligned in the same plane as the stem. Leaves radiate evenly from either side of the nodes to form bisymmetrical pairs of semicircular lobes, each lobe with 4-7 leaves. Proximal and distal leaves in each lobe shorter than the central leaves.

Description

The holotype (Fig. 8A) is an articulated stem bearing three complete pseudo-verticels of leaves and fragments of another group. Portions of a leaf group of an adjacent stem occur on the edge of the block. Stem 2 mm wide, with four prominent longitudinal ribs; internode length 28 mm. The groups of leaves on either side of the stem form bisymmetrical palmate lobes, each with 5 to 7 leaves, with a total of 10 to 14 at each node. Leaves in each lobe vary in length. The upper and lower leaves range from 20 - 30 mm long, the central leaves are longer, to 60 mm. Leaves are to 5 mm wide at widest point, one third to halfway from base; midrib 1 mm wide, continuous to acute apex.

The paratype (Fig. 8B) shows portions of three almost parallel stems, 1.5 - 2 mm wide and with internodes from 25 - 30 mm long; 5 to 7 leaves in each lobe on either side of the node. Leaves from 10 - 60 mm long. Some leaves show irregular transverse fractures and striations. which I believe are artifacts of preservation resulting from the shrinking of leaves with delicate structure and high water content.

Holotype

AMF112489, Paratype AMF112490, Australian Museum, Sydney.

Type Locality

Coalmine Quarry, Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

Other material

AMF112491, Reserve Quarry.

Name Derivation

Nymbolaria - contrived name, referring to the *Lobatannularia*-like plant from Nymboida.

tenuicaulis - from the Latin - slender stem.

Discussion

Nymbolaria tenuicaulis is a very rare plant in the Nymboida fossil flora. The type specimens were recovered with great difficulty from beneath a large fallen boulder weighing at least two tonnes. They were preserved as carbonised impressions on a grey mud smear beneath a massive sheet sandstone. From a narrow gap beneath the block it was just possible to see the *N. tenuicaulis* plants covering the whole under-surface. They appeared as a series of sub-parallel stems up to half a metre in length with little diminution in the thickness of the axes or the size of the pseudo leaf whorls over that incomplete length. The growth form as suggested by these fossils was of floating foliage shoots of a semi-aquatic plant or perhaps prostrate scrambling plants which colonised an open mud surface. Another possibility is that the fossils were foliage bearing branches attached to larger stems. However I consider it is unlikely that the slender stems of *N. tenuicaulis* would be sufficiently strong to form self supporting aerial foliage shoots.

Some species of the Northern Carboniferous genus *Annularia* (Walton 1936; Boureau 1964) and the Gondwana Permian genus *Lelstotheca* = *Stellotheca* (Surange and Prakesh 1962; Rigby 1966; McLoughlan 1992; Holmes 1995) are superficially similar to *N. tenuicaulis* but the former differ by their leaves forming complete symmetrical whorls in which the leaves fuse to form a narrow disc around the stem (Taylor and Taylor 1993). Plants included in *Annularia* from the Permian of Patagonia (Archangelsky 1960) and from Brazil (Rösler 1974) would be better placed in *Lelstotheca.*

Austroannularia, a sphenopsid genus erected for stems bearing asymmetrical leaf whorls from the Permian of Australia and Tibet (Rigby 1989), differs from *N. tenuicaulis* by the reniform shape of the verticels which are not divided into two separate lobes.

Lobatannularia from the Sub Angara and eastern Asian floras (Boureau 1964; Kim and Kimura 1988), ranges from the Permian to Late Triassic. It has groups of leaves at the nodes divided into two bisymmetrical lobes as in *Nymbolaria*, but differs by the oblanceolate leaves, often with a recurved attachment to the axis. The branching of the foliage shoots and the coherent, fan-shaped terminal leaf group of *Lobatannularia* is not present in the *Nymbolaria* material.

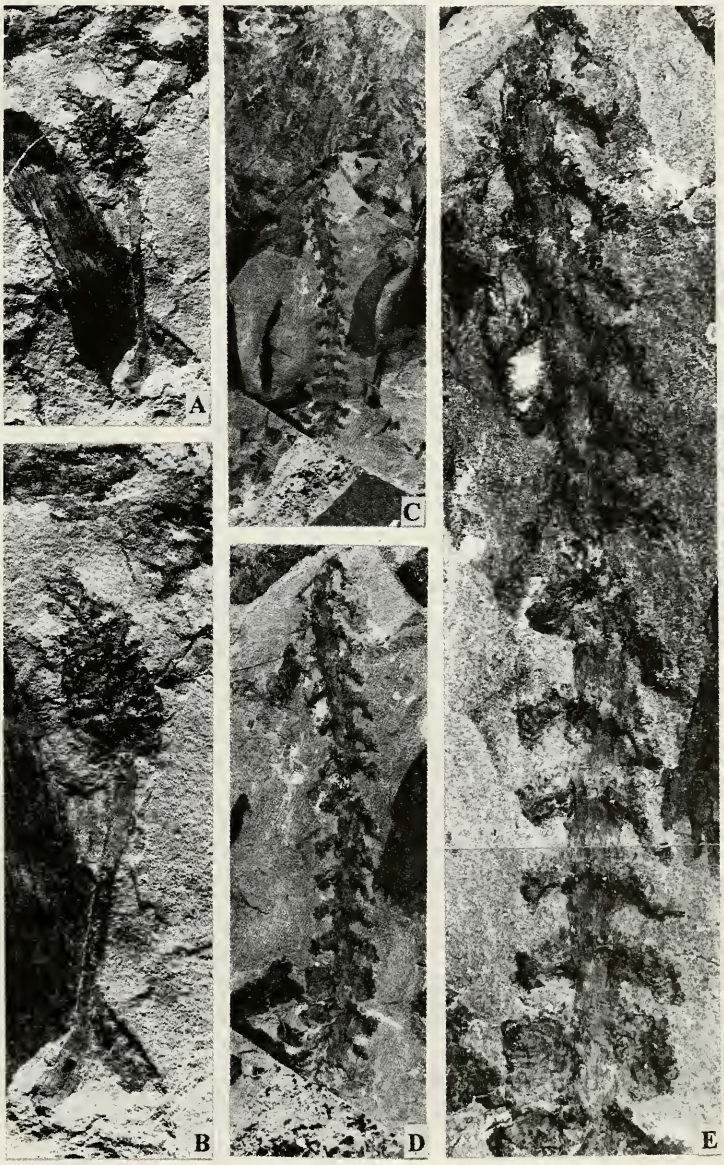

Figure 9. (A&B). ?Equisetalean strobilus cf. *Neocalamostachys* sp. A). AMF113367-8. B). x2. Reserve Quarry. (C-E). *Nymbotheca verticillata* gen. et sp. nov. Holotype AMF106757. C). x1. D). x2. E). x5. Reserve Quarry.

? Equisetalean strobilus cf. *Neocalamostachys* sp.*A*.
Figures 9A,B.

Description

A detached fructification consisting of a strobilus borne on a straight peduncle 3.5 cm long and 2 mm wide. The cone or strobilus is obovate in outline, 20 mm long, 9 mm wide in the proximal half and tapering distally to a more open and perhaps less mature apex. Near the base, the thick carbonised mass shows some rounded objects (? sporangiophores) c. 1.5 mm in diameter. Towards the apex of the strobilus smaller rounded objects are attached to slender pedicels which are arranged at right angles to the axis.

Material

AMF113367, Coalmine Quarry

Discussion

The absence of cuticle and spores at Nymboida is a limiting factor in determining the nature of this fertile organ. On the basis of the gross morphology of a cone or strobilus on a long pedicel, bearing ?sporangiophores not separated by bracts, this isolated organ is compared with *Neocalamostachys. Neocalamostachys* cones attached to *Neocalamites* stems have been reported from the Upper Triassic of U.S.S.R and Japan (Boureau 1964) and detached cones from Argentina (Brea and Artabe in press).

A line drawing showing several portions of linear segmented structures referred to *Calamostachys* sp. by Shirley (1898, Pl.18, Fig.4) indicates no features in common with cf. *Neocalamostachys* sp. described above. The cone of *Equisetites*? from the Late Triassic Ipswich Coal Measures of Queensland (Jones and de Jersey 1947, Text Fig.1, Pl.1, Fig.1) is problematical. The large ovate receptacle with its surface covered with pentagonal or hexagonal 'cells' may represent the fructification of a plant quite separate from the Equisetales.

Genus *Nymbotheca* nov. sedis incertae.
Nymbotheca verticillata gen. et sp. nov.
Figures 9C-E, 10A-D, 11.

Combined Diagnosis

A fertile organ consisting of a stout axis bearing regularly-spaced, entire, concave-convex, inverted shallow bowl-shaped, stem-encircling discs. Sessile broad-ellipsoidal sporangia covering the convex surface of each disc. Sporangia marked with a network of longitudinally elongated cells.

Description

Two specimens have been collected, one from each quarry site. Both are preserved as longitudinal sections of a partially compressed mid-portion of an incomplete axis. The holotype is 45 mm long and with a uniform width of c. 0.2 mm throughout the length preserved.The base and apex are missing. Sixteen stem-encircling discs c. 0.6 mm in diameter are spaced evenly, 0.3 mm apart, throughout the preserved length of the fossil. Portions of two discs have been flattened in the same plane as the axis and appear as roundish impressions. The other discs are preserved as concave-convex cross-sections at right angles or obliquely to the axis. Several of the discs bear on their convex surface, closely spaced, sessile, broad-ellipsoidal sporangial sacs c. 0.75 mm long and 0.5 mm wide. The surface of some of the sacs (Fig.10B) shows a network of longitudinally elongated cells. The method of attachment and orientation in life of this fertile axis is uncertain. Alternate reconstructions to show the organ as pendulous or erect are shown in Figs 11B and 11C.

Holotype

AMF 106757, Paratype AMF113368-9, The Australian Museum, Sydney, Australia.

Type Locality

Reserve Quarry, Nymboida. Paratype from Coalmine Quarry, Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

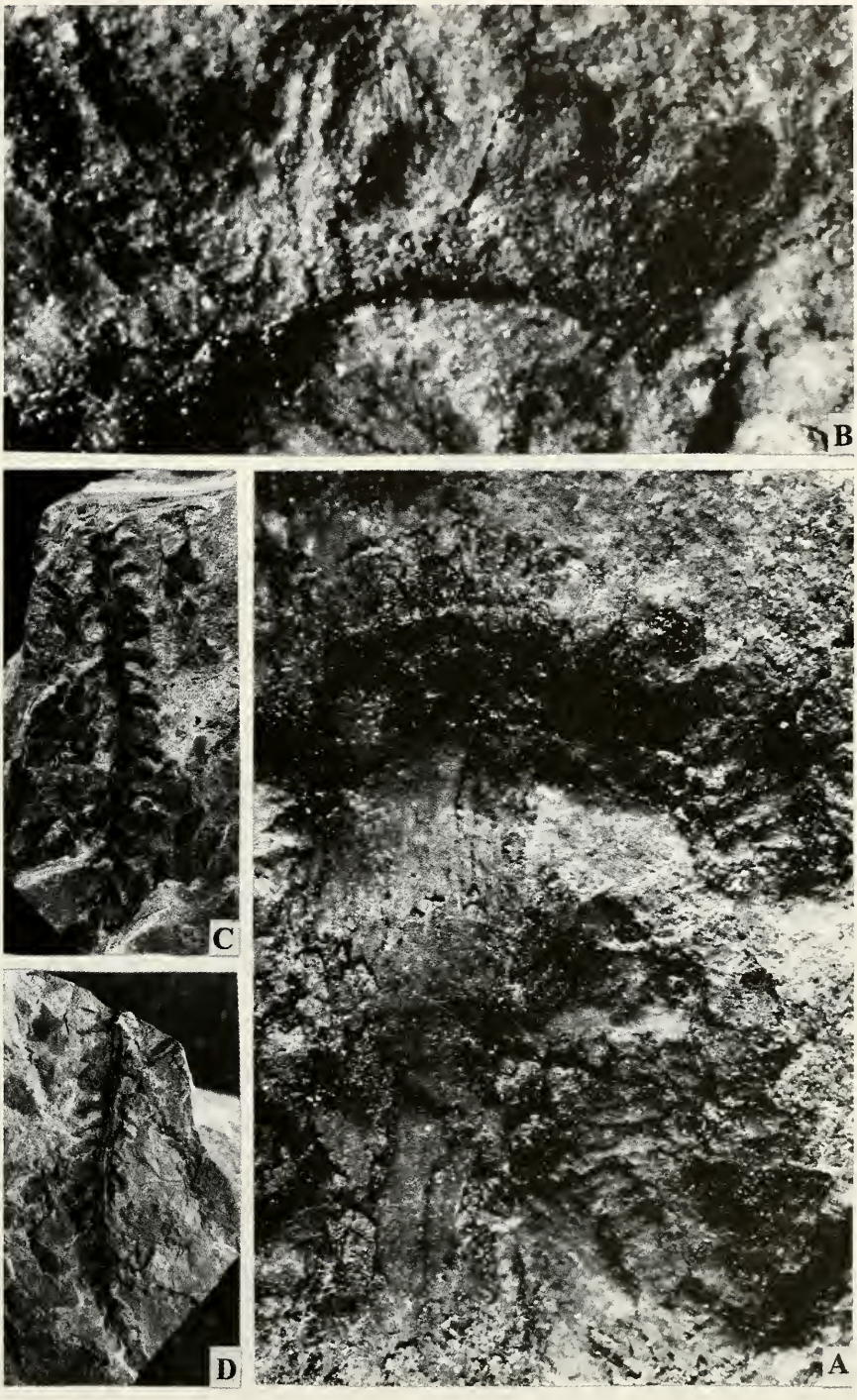

Figure 10. (A-C). *Nymbotheca verticillata* gen. et sp. nov. Holotype, AMF106757. Reserve Quarry. A).x10. B). x20. C). x1. Note striated walls on sporangial sacs. C, D). Paratype, AMF113367-8, part and counterpart. Coalmine Quarry.

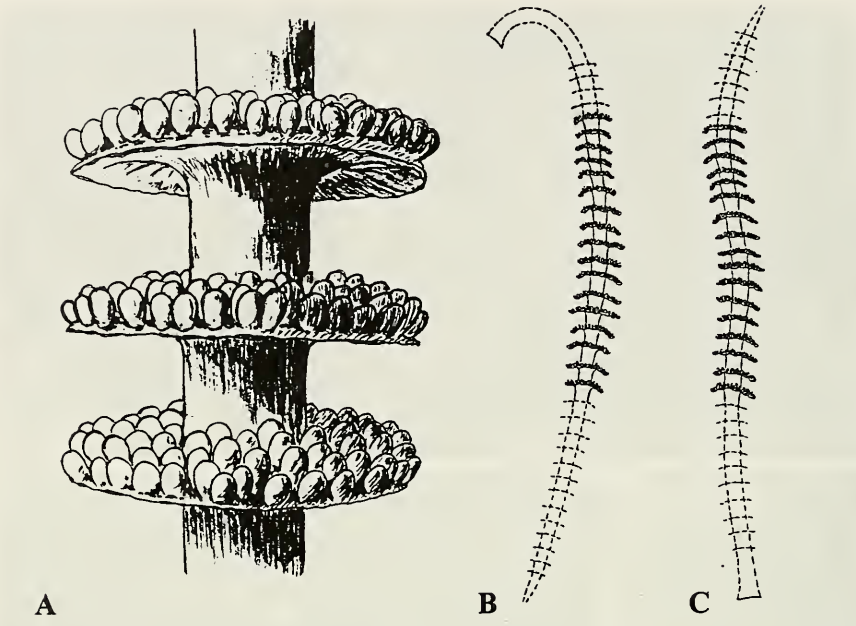

Figure 11. *Nymbotheca verticillata* gen. et sp. nov. (A). Reconstruction of a portion of a fertile axis. x8. (B,C). Alternate reconstructions of attachment in life. B). As pendulous. C). As erect.

Name Derivation

Nymbotheca - a contrived name for "Nymboida fertile organ".

verticillata - from Latin *verticillus* "whorl of a spindle" referring to the encircling discs on the axis.

Discussion

A fertile axis comprising a series of verticillate discs bearing sporangia over the whole surface of the disc is an architectural form not present in extant plants. It is, however, a distinguishing feature of the Order Discinitales in the Noeggerathiophyta, a little understood group of plants occurring as fossils from the late Carboniferous to the Triassic Period of the northern hemisphere (Boureau 1964; Taylor and Taylor 1993). The genera *Discinites* and *Saarodiscites* were erected for large cones with axes bearing stem-clasping discs. Sporangial sacs were closely spaced over the upper surface of the discs. In gross form, *Discinites* and *Saarodiscites* differ from *Nymbotheca verticillata* only by their larger size, less robust axes and by their closely spaced discs with upturned serrate margins. *Discinites* spp. are heterosporous (Nemejc 1937) and *Saarodiscites* is probably so (Hirmer 1940). This feature cannot be determined in *Nymbotheca verticillata* due to the absence of preserved spores, pollen grains and cuticle in the Nymboida material (deJersey 1958). *Discinites* cones have been found in close association with *Palaeopteridium* (Nemejc 1937) and *Russellites* (Mamay 1968). *Saarodiscites guthoerlii* has been found in close association with fronds of the foliage genus *Saaropteris* (Hirmer 1940). The holotype of *Nymbotheca verticillata* occurs on the same horizon as tiny fragments of *Dicroidium* and *Lepidopteris* leaves, the paratype is in a coarser siltstone and not associated with other remains. The reproductive organs of *Dicroidium* and *Lepidopteris* are well-known and differ significantly from those of *Nymbotheca verticillata* (Thomas 1933; Harris 1937; Holmes 1987; Anderson and Anderson 1989). Several undescribed forms of fern-like foliage occur at the Nymboida localities but none at present can be affiliated with *Nymbotheca verticillata.*

Sphenophyllostachys, which includes *Bowmanites* (Boureau 1964) of the Sphenophyllaceae, is an organ genus which includes a diversity of cones of plants bearing *Sphenophyllum* foliage. Species are characterised by the arrangement of the sporangia in the axil or on the upper surface of fertile verticillate and segmented bracts. *Sphenophyllostachys* is recorded from the Carboniferous of the northern hemisphere. *Cingularia,* in the Calamitaceae, is a genus for cones of plants bearing *Asterophyllites* foliage. The cone is an axis bearing verticels of sporangiophores with or without an accompanying sterile bract (Boureau 1964). Each sporangiophore has four striated sporangia attached in two pairs abaxially on the distal end of the fertile bract. *Cingularia*, also, is restricted to the Carboniferous of the northern hemisphere. By the evolutionary process of fusion and reduction of the fertile bracts into entire discs and by the transposition of the sporangia over the whole surface of the disc it may have been possible to derive *Nymbotheca* from *Sphenophyllostachys* or *Cingularia*. However, their wide separation geographically and in time suggests that their affinities, if any, to *Nymbotheca* would be extremely remote.

Two sphenophytes from the Gondwana Permian, *Ranigangia* spp (Rigby 1962) and *Phyllotheca etheridgei*, as reconstructed by Saksena (1954), have leaves conjoined for much of their length to form disc-shaped whorls with serrate margins. No fertile remains of either genus are known.

Phyllotheca australis stems, both with and without foliage, are widespread and abundant in the Gondwana Permian. The only recorded fertile specimen of *Phyllotheca australis* which was collected from the Permian Newcastle Coal Measures, was described by Townrow (1955). Groups of eight sporangia were borne terminally on twice forked peduncles which were attached in whorls directly to the axis above the axil of a segmented foliar bract. Some doubtful vegetative material comprising only stems and foliage from the Triassic has been placed in *Phyllotheca australis* by Walkom (1915, 1925), Frenguelli (1944c) and Artabe (1985). If *Phyllotheca australis* did persist into the Triassic, fertile specimens as per Townrow (1955), when compressed, would look very different to *Nymbotheca verticillata.*

Based on material from the Upper Triassic of Argentina, Menendez (1958, Pl.2, Fig.10) illustrated the internal cast of a hollow *Equisetites quindecimdentata* stem with a series of nodal diaphragms preserved in their original position within the stem. This 'cone' like arrangement of 'star-cap' diaphragms is superficially similar in form to the verticillate arrangement of *Nymbotheca*, but without the stout axis.

On the basis only of the superficial articulated nature of the axis, I have included this taxon doubtfully in the Sphenophyta. As presently known, *Nymbotheca verticillata* is an enigmatic fructification of doubtful affinities but on gross morphology is closest to the Discinitales in the Noeggerathiophyta of the northern hemisphere. It is unique in Gondwana Triassic plant assemblages.

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